Sound production of spawning lake sturgeon (*Acipenser fulvescens* Rafinesque, 1817) in the Lake Winnebago watershed, Wisconsin, USA

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Summary

The primary goal of this study was to obtain accurate data of previously undocumented lake sturgeon (*Acipenser fulvescens* Rafinesque, 1817) spawning sounds, generated during wild sturgeon reproduction. Biologists have long known that lake sturgeon produce low-frequency sounds during spawning bouts; energy from these sounds can break the surface of the water occasionally and propagate harmonics in the terrestrial atmosphere, creating a faint drumming popularly known as 'sturgeon thunder'. Understanding the contribution of this sonic behavior in context is essential for gaining a more comprehensive scientific appreciation of the process of sturgeon spawning, and accurate acoustic data should prove useful for fisheries managers seeking to monitor or enhance sturgeon stocks for reproductive activity. Recordings were made at several locations on the Wolf and Embarrass rivers during the 2011–2013 spawning seasons. Drumming sounds ranging from 5 to 8 Hz fundamental frequency were evident. Other characteristic noises associated with spawning lake sturgeon, including low-frequency rumbles and hydrodynamic sounds, were identified. Other high frequency sounds were also discovered. All of these sounds coalesce into a distinctive acoustic signature of lake sturgeon spawning activity. Knowledge of this sonic signature can be used to accurately document reproductive activity at multiple locations over extended periods using remote recording tools and techniques.

Introduction

Lake sturgeon (*Acipenser fulvescens* Rafinesque, 1817), are a species native to North America which were once widespread throughout the northeastern United States and Canada. Sizable populations survive in Wisconsin, where every spring, concentrations of these large fish travel miles up tributary rivers in the Lake Winnebago watershed to spawn. They gather on shallow riverbanks at favored locations, often in frenzied groups referred to as pods, vigorously mating for only a few days. These fish have been anecdotally known by biologists and sportsmen to produce low-frequency sounds during bouts of spawning, and local Menominee tribal traditions associating sturgeon with thunderstorms in the spring suggest an indigenous knowledge of sturgeon sound production during spawning that predates Western settlement. Sonic activity has been studied in other species of sturgeon (Tolstoganova, 1999; Johnston and Phillips, 2003); recently published studies have investigated frequency tuning in lake sturgeon (Meyer et al., 2010) as well as their hearing thresholds within certain frequencies (Lovell et al., 2005). A need for detailed scientific recordings and analysis of their low frequency spawning sounds has been noted in the literature (Meyer et al., 2010), as well as the need for field studies that can generate data on low frequency sound propagation by fish in shallow waters (Mann, 2006).

Acoustic behaviors in non-teleost fish are of interest from an evolutionary perspective, especially given the exceedingly long duration of the species on the planet, estimated to be around 150 million years. Assessing the cognitive abilities of fish and their organismal *Umwelt* has become a critical aspect in the comprehension of fish and their functioning within the environment. Acoustic communication studies done in the wild should have enhanced validity (Rosenthal and Lobel, 2006). Previous published research on sturgeon sound production has all been conducted in tanks, using methods to artificially stimulate the fish to produce sounds (Tolstoganova, 1999; Johnston and Phillips, 2003; Lovell et al., 2005; Meyer et al., 2010); an investigation conducted in the field that monitored the natural behaviors of the fish should provide important contextual information, more meaningful data from a fisheries management viewpoint, and counterbalance previous work.

The actual mechanism employed by *A. Fulvescens* in producing drumming sounds has not been confirmed, and the methods evolved by fish to produce sound are the most varied among vertebrates (Ladich and Fine, 2006). Several methods for specialized and unspecialized sound production have been recognized in fish (Kasumyan, 2008); three primary mechanisms identified in such pisciphony are hydrodynamic sounds; stridulation using bones or other sections of

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Many more images with associated sounds can be found in 'Interdisciplinary Adventures in Perceptual Ecology,' by Chris Bocast, Ph.D. dissertation, completed at the University of Wisconsin-Madison, 2014, available online through Proquest/UMI.

the body; and sonic muscles modulating the swimbladder (Tavolga quoted in Rosenthal and Lobel, 2006). Secondary methods include pneumatic sounds, particularly in physostomous fish; cavitational and respiratory noises; and percussive sounds generated by fish striking other surfaces with parts of their anatomy (Kasumyan, 2008). A portion of the study therefore focused on lake sturgeon anatomy, to ascertain any obvious sound production morphology. Several male and female lake sturgeon were dissected at different sites and times to identify any muscular structures around the swimbladder dedicated to sound generation. A large number of sonic muscles have evolved in the various 'drumming' teleost fish that have been studied (Ladich and Fine, 2006); since extrinsic sonic muscles have been speculated to have evolved before intrinsic muscles (Ladich and Fine, 2006), lake sturgeon were therefore expected to have some variant of Weberian apparatus or extrinsic sonic muscle attached to the swimbladder.

Sturgeon return to specific locations to spawn, swimming upriver to these sites when water temperatures reach 11.6°C, although tagging studies conducted by the Wisconsin Department of Natural Resources show that individual fish do not always return to the same spawning sites each year. This consistency in reproductive behavior facilitates field recording, as optimum monitoring locations can be predicted with reasonable accuracy, despite inter-annual variability in water levels. Hydrophones can be placed very near the fish without having to be in the water; however, this advantage is negated considerably by the actual spawning behavior of the fish, as the mating bouts are extremely vigorous and the fish can quickly wander from a positioned hydrophone or alternately run directly into it, making consistently productive gain settings on recording equipment a challenge. Nonetheless, several good examples of sturgeon drumming were obtained in April 2011, using a single passive hydrophone and basic professional audio gear.

These initial recordings were taken to Cornell's Bioacoustic Research Laboratory for spectrographic analysis. This presented some difficulty, due to the 44.1 k sample rate, but Dr. Ann Ward from Cornell University provided the necessary assistance with analysis. Results gave justification for further study.

Preliminary hypotheses, given the sexual size dimorphism of the fish (Ladich and Fine, 2006), and from field observations (Bruch and Binkowski, 2002), were that male sturgeon produced the drumming sounds. In most soniferous fishes, such sounds are produced either by some muscular structure in the mouth, pharynx, or drumming muscles utilizing the swim bladder as a resonant chamber and/or amplifier for the sounds. The preliminary lake sturgeon recordings were typical of sounds produced by fish using their swimbladder. Repetitive bursts of short duration and low frequency are produced by swimbladder mechanisms in fish species that have been investigated; these include the midshipman (Brantley and Bass, 1994; Bass and McKibben, 2003), types of toadfish (Fine et al., 2001; Modesto and Canario, 2003), varieties of catfish (Ladich, 1997), and haddock (Hawkins and Rasmussen, 1978), which are all teleost fish. Such drumming sounds appear to coordinate gamete release in other species of fish (Myrberg and Lugli, 2006).

Materials and methods

Experimental animals

Several fresh, legally-caught lake sturgeon were donated by spearfishers during the brief spearing seasons on Lake Winnebago in February 2012 and February 2013. The fish were examined at different sites around the lake; photos were taken of the dissections at the DNR registration station outside Wendt's on the Lake on 25 February 2012, and video was taken at the DNR registration station in Winneconne on 10 February 2013. The aims of the study were explained, the fish were weighed, measured, dissected and cleaned, and then returned to the fishermen. The length of the swimbladders was recorded; during the 2013 season, the length from the end of the swimbladder to the tip of the head was also measured.

Equipment

An in situ study was arranged for the spring of 2012 using an audio recording device capable of recording at low sample rates for more accurate low frequency spectral analysis, and a hydrophone capable of recording signals in frequency ranges down to 3 Hz. These primary recordings were made with a Wildlife Acoustics SM-2+ recorder, using 4, 8, 16, and 24 kHz sample rates, and a Wildlife Acoustics HTI 96-MIN active hydrophone with a sensitivity of −165 dB re: 1 V/uPa and a frequency response of 2 Hz to 40 kHz (flat to ±1 dB). Some stereo recordings were made in 2013 using the SM-2+ recorder and a second, identical Wildlife Acoustics hydrophone. Additional recordings were made with a Marantz PDM660 digital recorder, using a 44.1 kHz sample rate, and an Aquarian H2a-XLR passive hydrophone with a sensitivity of −180 dB re: 1 V/uPa and a frequency response of <10 Hz to 100 kHz (flat to ±4 dB 20 Hz–4.5 kHz); these proved invaluable for cross-checking data.

Numerous hydrophone placements and gain settings ranging from 0 to −36 dB on the Wildlife Acoustics recorder were tried. The most productive gain settings (i.e. good signal without clipping; minimal background noise) were from −9 to −18 dB; as the sounds of interest do not propagate well in the water and the spawning fish move constantly, no one setting proved ideal. Fish distances from the hydrophone ranged from 5 m to actually striking the hydrophone. Optimal results for analysis require a fairly strong initial signal; the process was necessarily hit or miss, with much recording time expended to obtain best-case samples. The hydrophone was generally placed between rocks to minimize current noise, not touching the bottom, and was sometimes extended using a PVC pipe, generally within half a meter of the shoreline, at depths of 0.25–1.0 m. The Aquarian hydrophone was placed in the water without extensions. Cable lengths in the water rarely exceeded more than half a meter. Average water temperatures were 11.6°C.

Software

Spectral analysis was done using Raven Pro 1.4 Build 45 on a MacBook Pro.

Results

Both male and female sturgeon were dissected, seeking any musculature dedicated to sound generation. Sturgeon swimbladders are large, averaging 23.85% of total length of the fish, with their location from the head of the fish averaging 27.27% total length. No extrinsic sonic muscles were found attached to the swimbladders. The swimbladders were also dissected but no intrinsic muscular structures were discovered.

Analysis of initial recordings at Cornell revealed a significant pulse of sonic energy at 100 Hz and well below. These sounds showed a harmonic structure in the drumming, indicating a fundamental frequency of 6 Hz, although the actual recorded signal did not extend that low (frequency range of Aquarian hydrophones does not extend below 10 Hz). In the 2012 and 2013 spawning seasons a large number of drumming sounds, anecdotally known as 'sturgeon thunder', were obtained; 36 optimal examples were later analyzed. The sturgeon drums consistently displayed a fundamental frequency ranging from ca. 5 to 8 Hz, with the main sonic energy concentrated generally in the second harmonic band (Fig. 1). Drumming sounds typically present energy in three to eight harmonics above the fundamental; the predominant sonic energy in all drumming recorded throughout the study remained below 100 Hz. Drums had an average duration of 3.03 s, with a bandwidth for 90% of the sonic energy averaging 49.5 Hz. Center frequency of this energy averaged 25.12 Hz, with a spread for 90% of the sound occurring between 6.80 and 61.26 Hz. Peak relative power measurements averaged 96.43 dB. All amplitudes were relative. While such rapid, low frequency pulses are characteristic of swimbladder sounds produced by teleost fish (Rosenthal and Lobel, 2006), sturgeon drums exhibit a much lower fundamental frequency. While in teleost fish the sonic muscle contraction rate has been found to correlate with the fundamental frequency (Ladich, 2004), how this relates to sturgeon is not clear.

Additional sounds consistent with spawning behavior were also documented. These sounds included very low frequency rumbles of lesser amplitude; these often immediately preceded a spawning bout (Fig. 2).

Characteristic hydrodynamic sounds were also found, and may have been amplified by the substrate at Keller Flats and particularly at Wood Duck (Fig. 3). Hydrodynamic sounds were observed to coincide with concentrated pods of spawning sturgeon and could extend for longer periods. These sounds can be very pronounced, depending on the site. Hydrodynamic sounds, combined with the sturgeon drumming, can sound much like actual thunder through a hydrophone.

Consistently appearing throughout all the recordings obtained through 2011–2013 were sharp knocks or raps, similar in tonal character to humans snapping their fingers or rapping a tabletop. Occurring singly or in periodic bursts (Figs 4 and 5), these sounds varied considerably in volume. These sounds were initially hypothesized as generated by sturgeon using a stridulatory mechanism. Individually, the raps exhibited a very consistent waveform while their sonic energy ranged from 800 Hz to 4 kHz, with many examples concentrated around 1.2 to 3.6 kHz. These sounds were often associated with spawning events, complicating the task of obtaining clear examples of sturgeon drumming. This was more pronounced in recordings made at higher sample rates and recordings done late at night. Rapping varied in the level of activity from site to site.

Hours of field recordings produced multiple examples that were problematic for a postulated stridulatory mechanism. The raps would at times rapidly increase in periodicity, resulting in
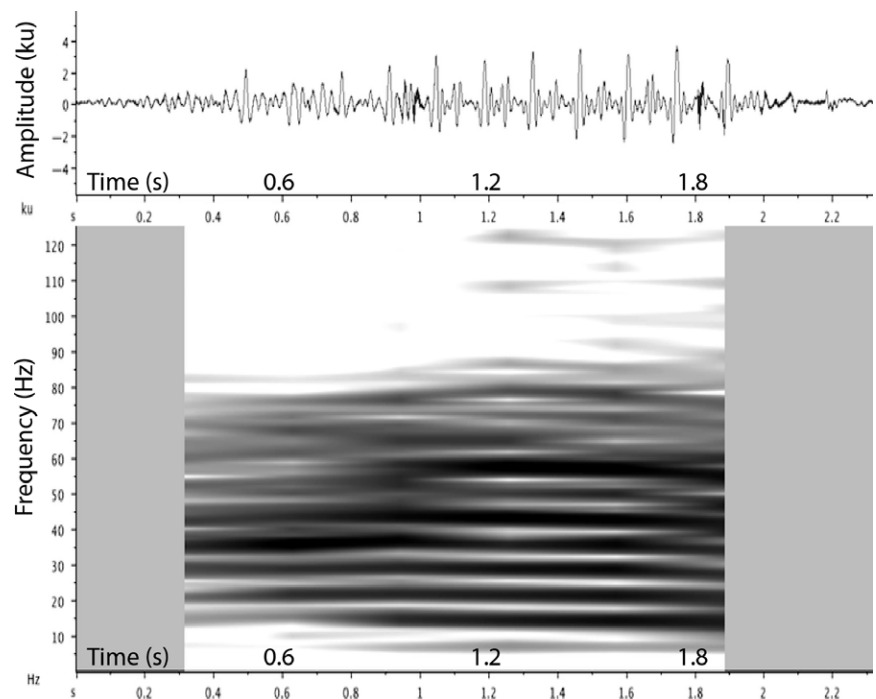

Fig. 1. Waveform and spectrogram of 7 Hz drum. Recorded at 4 kHz sample rate/Wood Duck site. Hann window spectrogram: size – 2514 samples, 3 dB filter bandwidth – 2.29 Hz.
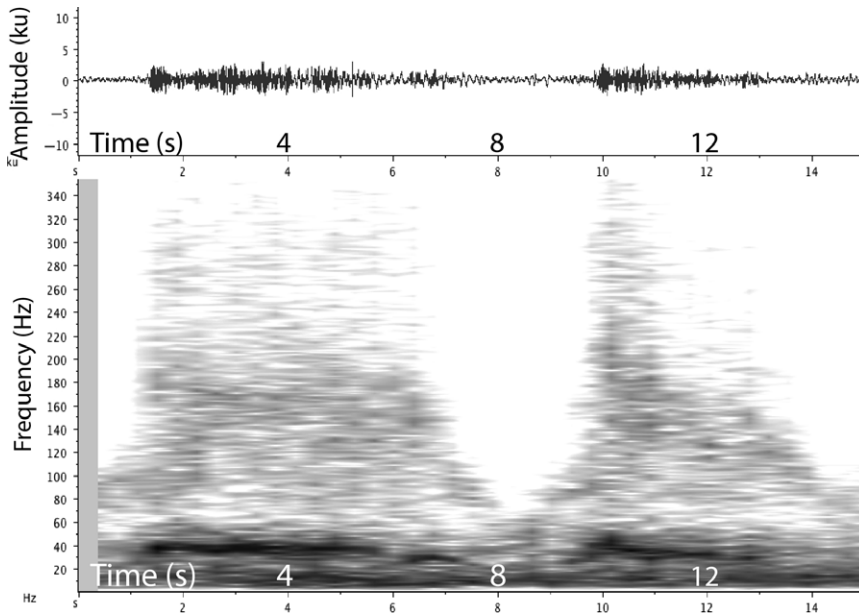
Fig. 2. Waveform and spectrogram of low frequency rumbles. Recorded at 8 kHz sample rate/Pearl Flats site. Hann window spectrogram: size – 6022 samples, 3 dB filter bandwidth – 1.91 Hz.
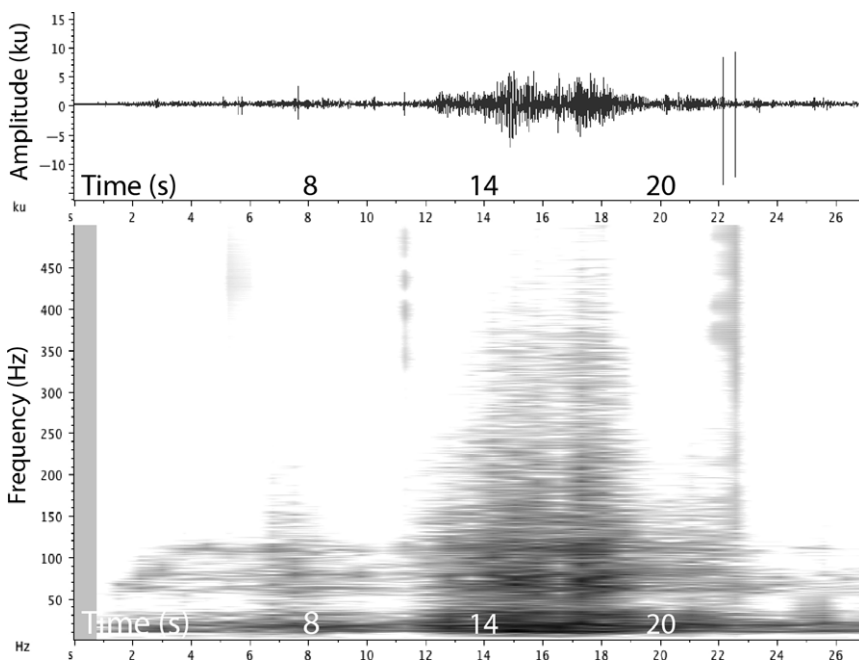

Fig. 3. Waveform and spectrogram of hydrodynamic sounds. Recorded at 4 kHz sample rate/Wood Duck site. Hann window spectrogram: size – 6022 samples, 3 dB filter bandwidth – 0.955 Hz.

a crisp crackle (Fig. 6). This crackling, which extends in frequency much higher than any of the other sounds, was also documented in stereo recordings from May 2013, with hydrophones set approximately 17 m apart. The crackling appears to move downriver, presumably with a fish (Fig. 6). Lower frequency sounds in the spectrogram are not biological.

Very unusual modulated tones were documented as well, although infrequently. Rapping and crackles preceding a spawning bout sometimes coalesced into a squeaky pitched tone (Fig. 7). Close analysis of the waveforms revealed sharp pulse spikes at high resolution. Similar examples demonstrated comparable characteristics, compensating for sample rate differences.

This final example of sturgeon sounds is a tone hypothesized to be associated more with pre-spawning sturgeon behavior (Fig. 8). This whistle, sonically resembling a dolphin or human whistle, appears to originate from another set of brief, low frequency pulses about 0.05 ms apart. Unlike cetacean whistles, this sound revealed no harmonic banding at any resolution. The waveform exhibits an unusual character as well, as the tone, although nearly identical to a human whistles in sound and wave-shape, varies from positive to negative amplitude. In addition, this lake sturgeon whistle bears much similarity to waveforms of high frequency tones produced by Russian sturgeon (Tolstoganova, 1999), which were also associated with pre-spawning behavior.
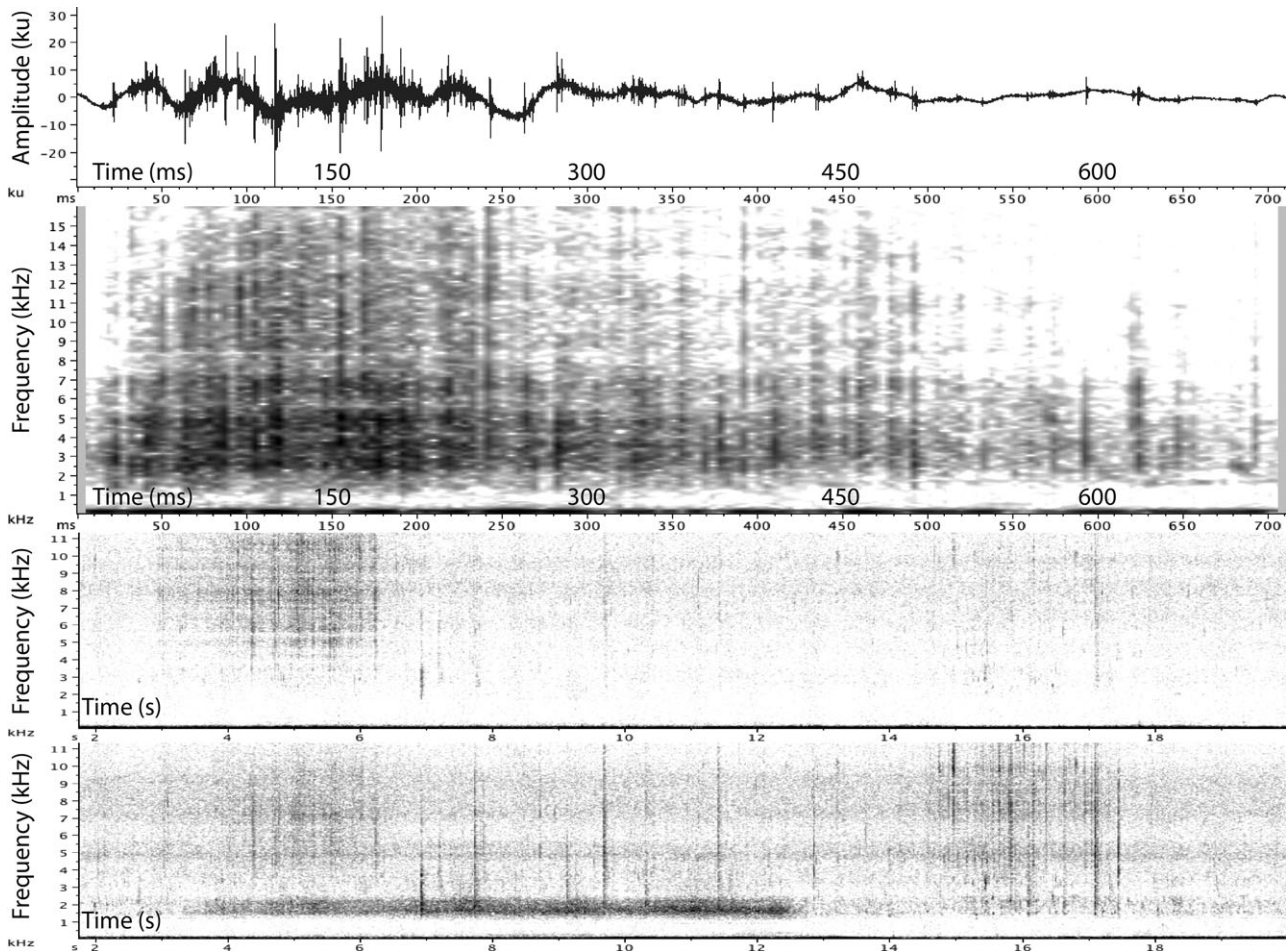
Fig. 4. Waveform and spectrogram of periodic rapping. Recorded at 4 kHz sample rate/Pearl Flats site. Hann window spectrogram: size – 598 samples, 3 dB filter bandwidth – 9.62 Hz.

Discussion

Concerns have been voiced regarding the possibility of much of the sophistication of communication between fish being overlooked by not studying them in their natural environment (Rosenthal and Lobel, 2006), as well as the possible constraining of sonic repertoire by fish in captivity (Midling et al., 2002). Although lacking some elements of precision, field recordings are also somewhat easier to confirm independently than laboratory experiments. Very low frequency sound production in lake sturgeon is surprising, given their preference for spawning in very shallow areas (1–2 m); due to high background noise and poor wave propagation, sounds below 100 Hz would not appear to be useful for organisms in this environment, although it has been observed that many fish do indeed produce sounds in these habitats (Lugli, 2002). Of the drumming sounds produced by previously studied fish, the fundamental frequencies varied between 50 and 250 Hz, usually with much of the sound energy contained in the first harmonic (Ladich and Fine, 2006). However, field observations of spawning lake sturgeon by DNR biologists Dan Folz and Michael Primising noted that net handles in the water would vibrate with their

drumming (Kline et al., 2009); this is consistent with the presence of extremely low frequency sounds. The drums are clearly made by the fish; the vigorous thrashing that accompanies lake sturgeon sound production is unambiguous, and there were no other fish sighted nearby. Quite likely the considerable size of the breeding fish, and proportionately their swimbladders, figures in these very low frequencies (Rosenthal and Lobel, 2006). If the fish do strum the bladder with some element of their internal structure, these sounds would be further limited in contraction rate, and by the amount of available air within the organ. The lack of any evident sonic muscle in lake sturgeon remains a physiological puzzle. As the fish are plainly engaging their entire body in the sound production, the pitch may be subject to the considerable mass and length of the fish (sturgeon can grow to 2.5 m or more in length and can weigh in excess of 90 kg). Spectrograms of the drumming support the hypothesis that the swimbladder, due to size and position within the fish, results in more sonic energy in harmonics rather than fundamental frequencies. This concentration of energy in higher harmonics has been noted in other organisms known to produce very low frequency sounds.[1] Natural variance in body size
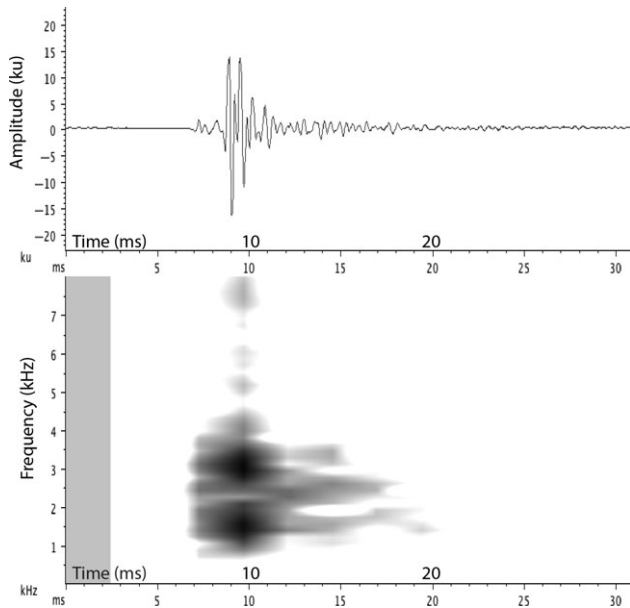
Fig. 5. Waveform and spectrogram of single rap. Recorded at 44.1 kHz sample rate/Wood Duck site. Hann window spectrogram: size – 214 samples, 3 dB filter bandwidth – 296 Hz.
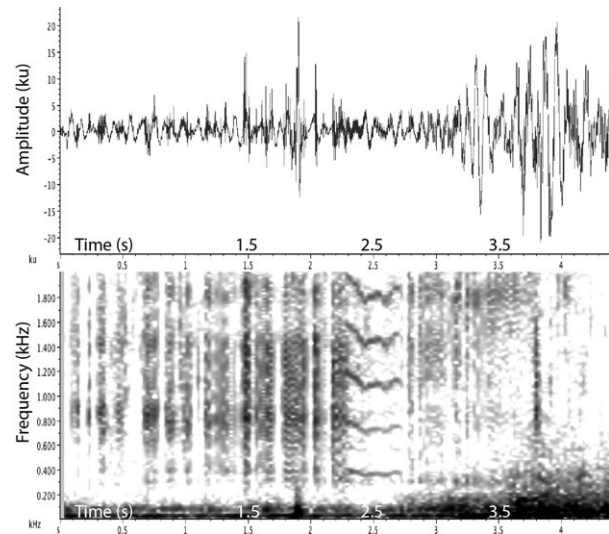

Fig. 6. Waveform and spectrogram of crackling. Recorded at 44.1 kHz sample rate/Wood Duck site. Hann window spectrogram: size – 402 samples, 3 dB filter bandwidth – 158 Hz. Stereo spectrogram recorded at 24 kHz sample rate/Shawano Bridge site. Hann window: size – 890 samples, 3 dB filter bandwidth – 38.8 Hz. The low pitch is not biological.

and bladder shapes likely contributes to occasional drums being produced that do not contain much harmonic information.

The mechanism for the drumming remains speculative at this point, given that the sturgeon must be relying on a less specialized method for sound production than sonic muscles. It has also been observed that not every thrashing lake sturgeon will produce an audible drumming. How the drumming sounds are perceived is unconfirmed. Fish are known to be sensitive to both particle accelerations (Sand and Bleckmann, 2008) and infrasound (Enger et al., 1993; Popper and Schilt, 2008), which can be sensed by the otoliths (Cotter, 2008). Previous research has observed sturgeon in the field responding to drumming from distances of up to 5 m (Bruch and Binkowski, 2002).

Stereo recordings from 2013 indicate that sturgeon drums can be measured from a few meters distance underwater. We hypothesize that lake sturgeon drumming acts like a shock wave, perceptible in the near field range, stimulating the fish through both direct hearing and lateral line stimulation. This sonic activity should aid the sturgeon in timing gamete release to ensure more successful reproduction, while attracting multiple individual males to spawn, increasing genetic diversity. Other characteristic aspects of signaling – dominance, territoriality, etc. – may also play a role in sturgeon spawning.

The possibility of the hydrodynamic sounds being 'Aeolian' artifacts of the hydrophone was discounted, as the sounds occurred at varying volumes consistent with different spawning locations. A hydrophone placed downstream at 15 m intervals captured the hydrodynamic sounds coincident with spawning bouts at correspondingly diminishing volume up to 60 m downriver, indicating that these sounds can also propagate past the near-field. Scientific understanding of the
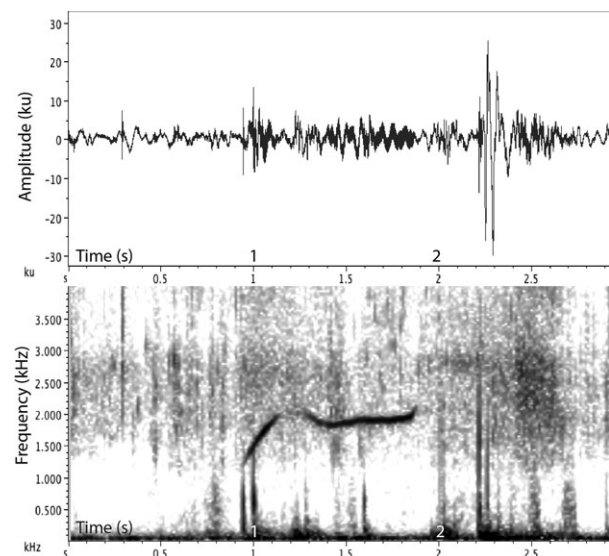

Fig. 7. Waveform and spectrogram of modulated tone. Recorded at 4 kHz sample rate/Wood Duck site. Hann window spectrogram: size – 231 samples, 3 dB filter bandwidth – 24.9 Hz. Tone exhibits a fundamental frequency around 350 Hz.

role of hydrodynamics signals in fish communication is in an embryonic stage; however, the hydrodynamic sounds from the converged fish could serve as an additional advertisement of spawning, also in combination with other characteristic sounds. These hydrodynamic sounds could help provide a recognizable audio signal above the very low frequencies of the drumming that can be used by biologists wishing to document spawning events using audio recording.

The raps presented a further conundrum. As noted, they were assumed to have been created using some sort of
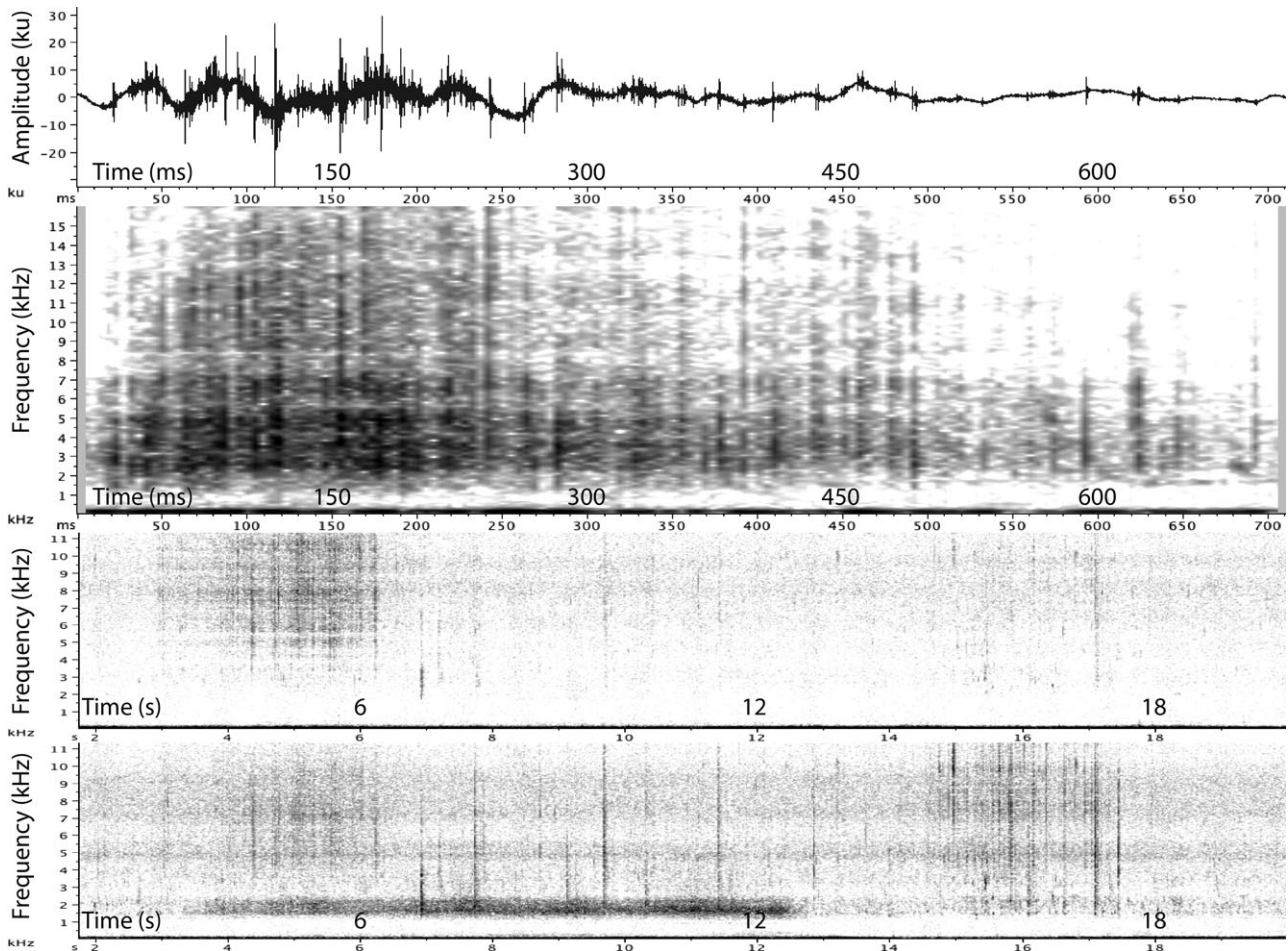
Fig. 8. Waveform and spectrogram of whistle. Recorded at 44.1 kHz sample rate/Diemel's site. Hann window spectrogram: size – 1226 samples, 3 dB filter bandwidth – 51.7 Hz. Note lack of harmonics.

stridulatory mechanism, and ancillary to the sturgeon drumming. However, they are in a register that may be above the range of sturgeon hearing. Popper has argued that sturgeon are hearing generalists, perceiving sounds up to 1000 Hz or so (Popper, 2005). Popper (2005) also raised this as a question of potential interest regarding previous studies documenting captive sturgeon producing sounds above 1 kHz.

The crackling examples bear some similarities to spectrograms of frequency jamming documented in brown ghost knifefish, *Apteronotus leptorhynchus* (Tallarovic and Zakon, 2005). These extend up to 12 kHz; again, out of range of expected hearing for lake sturgeon. The examples where raps accelerated into modulated tones presented a further explanatory challenge. The sounds themselves eventually provided a clue, being reminiscent of radio static. Comparisons to actual atmospheric static electricity recorded by mountaineers showed them to be quite similar, spectrographically as well as sonically. Additional comparisons were done with recordings of other fish known to produce electric organ discharges (EODs). The raps were very close in duration and waveshape (0.1 s, 1–6 phases of alternating polarity) to EODs produced by *Gnathonemus petersii*, the elephantnose

fish, while the modulated portions bore some resemblance sonically, spectrographically, and in the shape of their waveforms, to EODs produced by electric catfish, *Malapterurus electricus*. The audio data strongly suggests that the sturgeon are producing pulse-type EODs, typical of those emitted by what are known as the 'weakly electric' fish species. The unusual modulated tones might then be explained as the build-up of electrical charge around the animals, and not produced directly by the sturgeon, though how this could be maintained in running water is not clear.

An electric component in the sonic activity was unexpected. However, sturgeon have long been known to be electro-receptive (Moller, 2006). Sturgeon forage and breed successfully in murky waters and at night; late night recordings have demonstrated a great deal of these rapping sounds. Auditory and other cues are known to frequently accompany electrical signaling in other fish (Moller, 2002). Why EOD in sturgeon has not been identified before is not clear; these signals may only be produced in quantity during the spawning season, when stimulated by hormones. Recent studies have documented changes in electrocommunication behavior and adult neurogenesis in brain regions associated

with electrocommunication in *Apteronotus leptorhychus*, and similar changes that occurred only during reproduction in *Brachyhypopomus gauderio* (Dunlap et al., 2013). The sturgeon raps are generally quite low in amplitude and could be easily overlooked or masked by other sounds. It remains a possiblity that these sounds are produced by some form of unidentified stridulatory mechanism. Thorough examination of sexually active sturgeon for electrogenesis would be an essential step in settling this question. If *Acipenser* does not exhibit specialized electrocyte cells, there are known species – the apteronotids – which use a different mechanism: an electric organ comprised of the axons of spinal electromotor neurons (Waxman et al., 1972). If these lake sturgeon sounds do come from electric discharges, the increased rapping recorded during spawning bouts would be expected, as the sturgeon's sensitive ampullary receptors are stimulated by vibrational frequencies below 30 Hz (Rose, 2004), and this would give a further biological impetus to produce very low frequency sounds during reproduction. A considerable element of bio-electricity may be involved in sturgeon spawning, as has been documented in other fish such as sting-rays (Hopkins, 2009). This may account for the rubbing behavior of sturgeon, gill flaring, and the massing together of the fish in spawning pods, as they may be modulating their electric field in a manner similar to catfish (Keller, 2004).

Only one certain example of the sturgeon whistle was documented in this study, yet Wisconsin fish biologists have known of its existence from amateur tapes recorded by local sportsmen and has also been reported anecdotally by reputable sources. It is included, as it exhibits some singular peculiarities. Suspected examples of sturgeon emitting whistles when under stress have been described by aquaculturalists in Europe. Such signaling raises a prospect of developing acoustic methods for more timely diagnosis of health in cultured sturgeon, as farmed fish often do not exhibit outward signs of sickness until it is too late to save them. Independent confirmation of pre-spawning whistling, as well as investigation of sturgeon electric signaling, are two research questions indicated by the results of this study.

The acoustic environment is a significant factor in the lives of fish (Cotter, 2008), and the soundscape of rivers may be central to many freshwater fish behaviors. Acoustic recordings of these soundscapes can yield temporal and spatial data for management, and identify breeding sites as being in-use or as holding conservation potential. Along with known physical cues from river temperature and substrate, lake sturgeon must synthesize visual, acoustic, and electrical sense information into an adaptable complement of wide-ranging sensory perceptions. This powerful suite of perceptions has undoubtedly assisted *A. fulvescens* in successfully propagating their species for over 150 million years.

Acknowledgements

Note

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